Bayesian Inference of Genetic Parameters and Selection Response for Litter Size Components in Pigs

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ABSTRACT

Three contemporary lines were formed from the progeny of 50 French Large White sows. In the first line, gilts were selected for ovulation rate at puberty. In the second line, they were selected for prenatal survival of the first two parities, corrected for ovulation rate. The control constituted the third line. Ovulation rate at puberty was analyzed using an animal model with a batch effect. Prenatal survival was analyzed with a repeatability animal model that included batch and parity effects. Flat priors were used to represent vague previous knowledge about parity and batch effects. Additive and residual effects were represented assuming that they were a priori normally distributed. Variance components were assumed to follow either uniform or inverted chi-square distributions, a priori. The use of different priors did not affect the results substantially. Heritabilities for ovulation rate ranged from 0.32 to 0.39, and from 0.11 to 0.16 for prenatal survival, depending on the prior used. The mean of the marginal posterior distribution of response to four generations of selection ranged from 0.38 to 0.40 ova per generation, and from 1.1 to 1.3% of the mean survival rate for average survival per generation.

LITTER size is difficult to improve by selection (Haley *et al.* 1988) unless high selection pressures are applied in large populations (Blasco *et al.* 1995). Selection for ovulation rate and prenatal survival have been suggested as indirect ways to improve litter size (Johnson *et al.* 1984). Only one selection experiment for ovulation rate in pigs and two in mice have been published, but although an improvement in number of ova released was obtained, no correlated response in litter size was observed. Selection for prenatal survival has been undertaken in pigs using an index that included ovulation rate and prenatal survival up to 50 days, and it was successful in improving litter size. No experiments on prenatal survival have been reported in pigs, but one experiment with mice showed promising results (see Blasco *et al.* 1993, 1995).

The objective of this paper is to report an analysis of response to selection from two experiments using French Large White pigs; one, for ovulation rate, and the other for prenatal survival. The results on the correlated response in litter size will be published separately.

Response to selection has traditionally been estimated using either least-squares procedures or mixed model techniques with animal models (Sorensen and Kennedy 1984). In either case, it is difficult to obtain a precise estimate of the sampling variance of the estimator of selection response. A Bayesian approach has been proposed by Sorensen *et al.* (1994) that takes into account the selection mechanism that generated the data and the uncertainty about fixed effects and variance components. Using this approach, the uncertainty about response to selection is described via its marginal posterior distribution, without resorting to approximations. This novel way of analyzing selection experiments is applied in the present work. The emphasis here is to incorporate prior information from the literature, which is combined with that arising from the experimental data. To check consistency of conclusions with other methods of inference, results from a least-squares analysis and from a restricted maximum likelihood/best linear unbiased prediction (REML/BLUP) procedure are succinctly presented.

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MATERIALS AND METHODS

Animals: Three contemporary lines (two selected and one control) were formed from the progeny of 50 French Large White sows from the INRA experimental herd of Saint-Gilles. Sows were artificially inseminated with semen from 25 boars from French artificial insemination centers. The experiment was conducted at the INRA experimental farm of Galle. From each line of each generation ~50 gilts and 6–8 boars from first litters were kept for breeding. Puberty was defined as the first estrus, detected by standing response to a teaser boar. Estrus detection on a daily basis was initiated at 150 days of age and continued until 250 days of age. Ovulation rate at puberty was estimated by counting the number of corpora lutea using laparoscopy on females under general anesthesia, between 10 and 15 days after mating. Females were kept for two litters distributed in seven farrowing batches per generation.

Four generations of selection were analyzed. In the first line

(S-OR), gilts were selected for ovulation rate (OR) at puberty. In the second line (S-PS), gilts were selected for prenatal survival corrected for ovulation rate (PS), using data from the first two parities. Prenatal survival was computed as follows (Bidanel *et al.* 1996):

$$I_i = \frac{1}{2}\sum_{j=1}^{j=2} 100\left[\frac{TNB_{ij}}{OR_{ij}} + 0.018(OR_{ij} - \overline{OR}_j)\right],$$

where TNB_{ij} and OR_{ij} are, respectively, the total number born and ovulation rate of female i in parity j, and $\overline{OR}_j$ is the mean of parity j. The experiment included a control line in which both traits were measured.

Models and statistical inference: Selection was performed for one trait in each of the two selected lines and, accordingly, traits were analyzed univariately. In each case, the relevant selected line and control line were analyzed jointly. The data from OR, $\boldsymbol{y}_{or}$, was assumed to be generated from the following conditional multivariate normal distribution:

$$\boldsymbol{y}_{or}|\boldsymbol{b},\boldsymbol{a},\sigma_e^2 \sim N(\boldsymbol{Xb} + \boldsymbol{Za}, \boldsymbol{I}\sigma_e^2),$$

where $\boldsymbol{b}$ is a vector of batch effects, $\boldsymbol{a}$ is a vector of additive genetic values, σ_e^2 is the residual variance, $\boldsymbol{X}$ and $\boldsymbol{Z}$ are known design matrices, and $\boldsymbol{I}$ is the identity matrix. Prenatal survival ($\boldsymbol{y}_{ps}$) was assumed to be conditionally normally distributed as follows:

$$\boldsymbol{y}_{ps}|\boldsymbol{b},\boldsymbol{a},\boldsymbol{c},\sigma_e^2 \sim N(\boldsymbol{Xb} + \boldsymbol{Za} + \boldsymbol{Wc}, \boldsymbol{I}\sigma_e^2),$$

where the vector $\boldsymbol{b}$ contains both batch and parity effects, $\boldsymbol{c}$ is a vector of permanent environmental effects, and $\boldsymbol{W}$ is a known design matrix. The remaining parameters have an interpretation equivalent to that in the model for OR. Preliminary analyses indicated that maternal effects did not contribute to variation in either OR or PS, and no association between OR and PS with age within parity could be detected. Thus, these effects were not included in the final model.

As mentioned before, the statistical analysis was carried out using a Bayesian perspective. This requires a judicious choice of prior distributions for all the parameters in the model. Invoking the infinitesimal model (*i.e.*, Bulmer 1980), additive genetic values for both OR and PS were assumed to follow a multivariate normal distribution

$$\boldsymbol{a}|\boldsymbol{A},\sigma_a^2 \sim N(\boldsymbol{0},\boldsymbol{A}\sigma_a^2),$$

where $\boldsymbol{A}$ represents the known additive genetic relationship matrix, $\boldsymbol{0}$ is a vector of zeros, and σ_a^2 is the relevant (*i.e.*, OR or PS) additive genetic variance in the base population from which the data were sampled. In the case of PS, the distribution of permanent environmental effects was assumed normal and of the form

$$\boldsymbol{c}|\sigma_c^2 \sim N(\boldsymbol{0},\boldsymbol{I}\sigma_c^2),$$

where σ_c^2 is the component of variance associated with permanent environmental effects. Improper uniform prior distributions were assumed to approximate vague prior knowledge about parity and batch effects in both traits.

Prior distributions for variance components were built on the basis of information from the literature. The approach followed to generate a prior distribution for the additive genetic variance is described below. The remaining components of variance were assigned prior distributions in a similar manner. For ovulation rate, most of the published research shows heritabilities of either ~0.1 or ~0.4, ranging from 0.1 to 0.6 (Blasco *et al.* 1993). Bidanel *et al.* (1992) reports an estimate of heritability of 0.11 with a standard error of 0.02 in a French Large White population. On the basis of this prior information for ovulation rate, and assuming a phenotypic variance of 6.25 (Bidanel *et al.* 1996), three different sets of prior distributions reflecting different states of knowledge were constructed for the variance components. In this way, we can study how the use of different prior distributions affect the conclusions from the experiment. The first set is an attempt to ignore prior knowledge about the additive variance for ovulation rate. This was approximated assuming a uniform distribution, where the additive variance can take any positive value up to the assumed value of the phenotypic variance, with equal probability. In set two, the prior distribution of the additive variance is such that its most probable value is close to 2.5, but the opinion about this value is rather vague. Thus, the approximate prior distribution assigns similar probabilities to different values of the additive variance of ~2.5. The last case is state three, which illustrates a situation where a stronger opinion about the probable distribution of the additive variance is held, a priori, based on the fact that the breed used in this experiment is the same as in Bidanel *et al.* (1992). The stronger prior opinion is reflected in a smaller prior standard deviation. Priors describing states two and three are scaled inverted chi-square distributions. The scaled inverted chi-square distribution has two parameters, v and S^2. These parameters were varied on a trial and error basis until the desired shape was obtained. Figure 1 illustrates the three prior densities for the additive variance for ovulation rate.

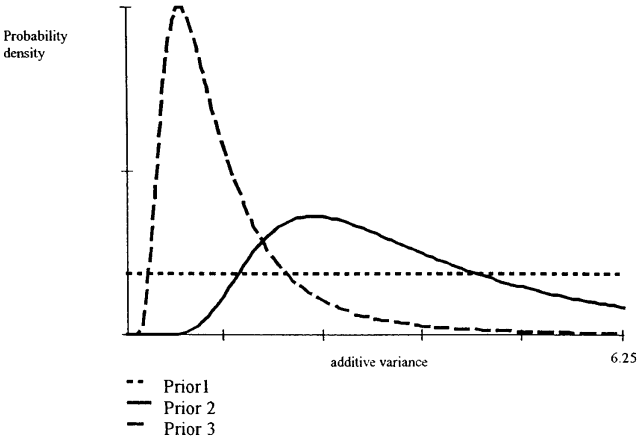

Figure 1.—Prior distributions for the additive variance of ovulation rate.

The same procedure was applied for prenatal survival. Here, prior distributions for variance components were built on the assumption that the phenotypic variance is 345 (Bidanel *et al.* 1996). The published heritabilities are centered at ~0.2, ranging from 0 to 0.23. Bidanel *et al.* (1992) gave a value of 0.03, with a standard error of 0.03 for French Large White pigs. The state of opinion one was represented using uniform priors for all variance components. In state two, similar probabilities of additive variance are assigned to values of ~70, and the state of opinion three assigns relatively high mass to values of additive variance near zero. These are shown in Figure 2.

The random variable genetic mean for a particular selected line (S-PS or S-OR) and generation, whose marginal posterior distribution we wish to obtain, was defined as the average additive genetic value among individuals belonging to that line and generation.

In order to draw marginal inferences about response to selection or other genetic parameters using the Bayesian approach, it is necessary to derive the relevant marginal posterior distribution. This requires performing multiple integrals that do not have analytically tractable solutions under the present models. To circumvent this problem, one can obtain Monte Carlo draws from the appropriate marginal posterior distribution using the Gibbs sampler. Details about the

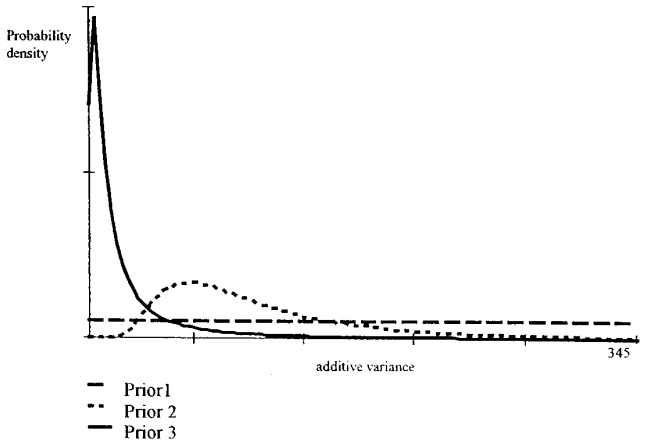

Figure 2.—Prior distributions for the additive variance of prenatal survival.

application of this technique in the analysis of selection experiments can be found in Sorensen *et al.* (1994). In the present work, the Monte Carlo estimate of the marginal posterior distribution of the genetic mean for a particular generation and line can be described as follows: first, in a particular round of the Gibbs sampling procedure, a draw was obtained from the joint posterior distribution of the vector of additive genetic values. Second, the additive genetic values belonging to the generation in question were averaged. This average constituted one sample from the marginal posterior distribution of the genetic mean. The number of rounds in which this was repeated was equal to the length of the Gibbs chain, and the resulting samples constitute Monte Carlo draws from the marginal posterior distribution of the genetic mean for the line and generation in question. The justification for interpreting the mean of the samples of additive values, as a sample from the marginal posterior distribution of the genetic mean, is based on standard results of Markov chains, and more details can be found in, for example, Gilks *et al.* (1996).

The final results of experimentation included in this work were obtained by averaging the results obtained from two independent chains, each of length 100,000. In each chain, the first 10,000 samples were discarded and thereafter saved every 30 iterations, thus keeping a total of 3000 samples. This strategy was arrived at empirically after studying the results of several different runs and satisfying the requirements obtained by applying Raftery and Lewis's (1992) method to obtain inferences about quantiles from marginal posterior distributions with a given level of precision.

Estimates of features of marginal posterior distributions were obtained directly from the Gibbs samples. The autocorrelation between samples and the Monte Carlo error of the estimates were computed using methods described in Geyer (1992).

RESULTS

The raw mean and standard deviation for OR, from the control line, were 12.97 and 2.28, respectively, based on 388 data points. The corresponding figures for PS were 65.56 and 18.35, based on 351 data points.

Table 1 shows the parameters (v, S^2) of the scaled inverted chi-square prior distributions of the variance components. The values chosen for these parameters generated a shape for these distributions that approximately reflects the information that was available from the literature before the experiment was conducted.

TABLE 1

Parameters of inverse chi-square prior distributions of variance components

Trait	Priors	v_a	S_a^2	v_c	S_c^2	v_e	S_e^2
OR	2	6.5	2.4	—	—	30	3.6
	3	6.5	0.6	—	—	30	5.4
PS	2	6.5	80	6.5	20	30	300
	3	2.5	32	6.5	20	30	348

OR, ovulation rate at puberty; PS, prenatal survival; v, S^2, parameters of the chi-square distribution; a, additive genetic effects; c, permanent environmental effects; e, residual effects.

Results from the Bayesian analysis can be found in Tables 2–5. The mean and standard deviations of the marginal posterior densities of heritability for OR and PS, and repeatability for PS, calculated using the three sets of prior distributions, are shown in Table 2. Estimates of the mean of the marginal posterior distribution of heritability for OR ranged from 0.32 to 0.39 and from 0.11 to 0.16 for PS, depending on the prior used. Estimates of the mean of the marginal posterior distribution of repeatabilities for PS range from 0.23 to 0.19. Table 2 also shows posterior standard deviations. These results indicate that three prior distributions that differ considerably lead to similar posterior inferences about heritabilities and repeatabilities.

Tables 3 and 4 show Monte Carlo estimates of means of posterior distributions of genetic means for OR and PS, respectively. Because of to the approximate normality of all the posterior densities (see Figures 3 and 4), it is simple to obtain estimates of posterior confidence regions from the data in the tables. In both cases, there is a clear indication that selection has been successful and the results are little affected by the prior distributions. For OR, the three sets of prior distributions lead to very similar posterior inferences. The response to

TABLE 2

Mean (m) and standard deviation (SD) of posterior density of heritability (h^2) and repeatibility (r) for ovulation rate at puberty (OR) and for prenatal survival (PS) in a French Large White population, obtained using three prior distributions

	Prior	m(h^2)	SD(h^2)	m(r)	SD(r)
OR	1	0.39	0.07	—	—
	2	0.39	0.06	—	—
	3	0.32	0.06	—	—
PS	1	0.12	0.06	0.23	0.05
	2	0.16	0.04	0.23	0.04
	3	0.11	0.04	0.19	0.04

TABLE 3

Monte Carlo estimates of means and standard deviations (in parentheses) of posterior densities of genetic means of generations one to four (G1–G4) for OR in the selected line (S-OR), calculated using the three sets of prior distributions

	Prior	G1	G2	G3	G4
S-OR	1	0.30 (0.31)	0.51 (0.35)	1.03 (0.39)	1.58 (0.43)
	2	0.31 (0.30)	0.51 (0.34)	1.05 (0.38)	1.55 (0.42)
	3	0.31 (0.31)	0.51 (0.35)	1.01 (0.35)	1.53 (0.38)

four generations of selection for OR has been ~0.40 ova per generation, >3% of the average per generation.

For PS, the posterior uncertainty of response is >OR. The 95% posterior confidence regions of total response (genetic mean at generation four) for prior sets one, two, and three are approximately (−1.35, 7.13), (−1.11, 8.09), and (−1.12, 6.92), respectively. Using prior set one, the empirical posterior probability that the genetic mean in the last generation was >0 is 95%. This was estimated computing the proportion of the Monte Carlo samples from the posterior density of the genetic mean in generation four that were >0. An estimate of the marginal posterior density of the genetic mean at generation four using prior set one is shown in Figure 4. An improvement of 3–4% of prenatal survival in four generations of selection implies a 1.1–1.5% increase of the average survival rate per generation. For both traits, we note that the posterior variance of the genetic means increases with each generation. This is a reflection of the correlation among additive genetic values that builds up as a result of genetic drift, which is captured by the Bayesian analysis.

TABLE 4

Monte Carlo estimates of means and standard deviation (in parentheses) of posterior densities of genetic means of generations one–four (G1–G4) for PS in the selected line (S-PS), calculated using the three sets of prior distributions

	Prior	G1	G2	G3	G4
S-PS	1	−0.53 (1.44)	1.23 (1.61)	2.83 (1.94)	2.89 (2.12)
	2	−0.64 (1.70)	1.50 (1.87)	3.46 (2.05)	3.49 (2.30)
	3	−0.46 (1.45)	1.22 (1.60)	2.84 (1.82)	2.90 (2.01)

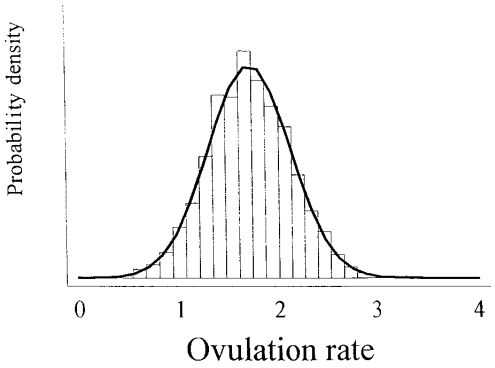

Figure 3.—Posterior density of the average breeding values in the last generation of selection for ovulation rate at puberty.

As we mentioned before, the results presented here are based on the average results from two independent chains. Computation of the Monte Carlo standard errors indicated that the estimates did not differ significantly between chains. To illustrate this point, Monte Carlo standard errors of the estimates of posterior means of heritability for OR and PS, repeatability for PS, and of the genetic means for OR and PS at generation four, are shown in Table 5. In all cases, the difference in estimates of posterior means between chains were $<10^{-3}$ for heritabilities and repeatabilities and $<10^{-2}$ for the estimates of the genetic means.

The data were also analyzed using least-squares and the "REML/BLUP" procedures. This was done to check for consistency of conclusions with alternative methods of inference and to contrast the Bayesian approach with the other two traditional approaches. The least-squares approach for both OR and PS was applied to a model that included generation and batch-nested within generation for OR, and parity number, generation, and batch-nested within generation for PS. The difference between the least-squares estimates of generation effects from the selected and control lines are shown in Table 6. The picture that emerges from OR is relatively clear: response to selection is effective with a total response

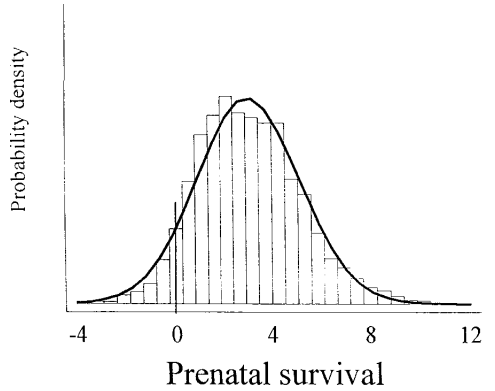

Figure 4.—Posterior density of the average breeding values in the last generation of selection for prenatal survival.

TABLE 5

Monte Carlo standard errors (SE) of the estimates of means of heritabilities (h^2), repeatabilities (r), and of the genetic means of generation four (G4) from lines S-OR and S-PS

	S-OR			S-PS		
	Prior 1	Prior 2	Prior 3	Prior 1	Prior 2	Prior 3
SE (h^2)	0.002	0.002	0.002	0.005	0.002	0.003
SE (re)	—	—	—	0.002	0.001	0.002
SE (G4)	0.018	0.023	0.021	0.120	0.087	0.182

of ~0.45 ova per generation. This is in agreement with the results from the Bayesian analysis. Prenatal survival is a more variable trait; the results are less clear and little can be concluded from this least-squares analysis. Sampling variances of the least-squares estimators cannot be obtained exactly, but approximations that account for genetic drift are available (*i.e.*, Hill 1980; Sorensen and Kennedy 1983). These were not computed in the present work. This erratic picture of selection response is often characteristic of the least-squares analysis.

The "REML/BLUP" approach is a two-step procedure, whereby genetic variances are estimated in the first step using restricted maximum likelihood, and are used in lieu of the true parameters to solve the mixed model equations in the second step (Sorensen and Kennedy 1986). Because of the "shrinkage" associated with this method, inferences about response to selection are often clearer than those obtained using least-squares. Further, in contrast to the least-squares procedure, the method can disentangle genetic and nongenetic trends in complicated data structures with overlapping generations. Two shortcomings of the procedure, however, are the following: first, that estimated variances are regarded as known parameters and no account is taken of the error of estimation. Second, the exact sampling distribution of the prediction of response to selection obtained with this procedure is not known. This makes it difficult to describe the error of estimation of response.

Residual maximum likelihood estimates of heritabilities for OR and PS have been reported in a preliminary analysis of the same data set by Bidanel *et al.* (1996). The heritability estimates given by Bidanel *et al.* (1996) are 0.36 for OR and 0.14 for PS, which is in agreement with the results reported here. Table 6 shows the evolution of the genetic means for both OR and PS using "REML/BLUP" with the above estimates. The results for OR are in agreement with those obtained using the Bayesian approach. The results for PS resemble the results obtained under the prior set two, but there is no theoretical reason for this similarity here. It is only in very large samples that there should be agreement between inferences based on "REML/BLUP" and the Bayesian approach.

TABLE 6

Estimates of genetic means using least squares (expressed as deviations between selected line and control line) for ovulation rate at puberty OR (LS) and for prenatal survival PS (LS), and using "REML/BLUP"-OR (R/B), PS (R/B)

	G1	G2	G3	G4
OR (R/B)	0.27	0.45	1.00	1.54
OR (LS)	−0.09	0.35	1.98	1.87
PS (R/B)	−0.54	1.49	3.26	3.42
PS (LS)	−5.71	2.11	4.13	−2.82

Generations one to four: G1–G4.

DISCUSSION

We have presented a Bayesian analysis of response to selection for ovulation rate at puberty and for prenatal survival in French Large White pigs. It is a characteristic of the Bayesian approach to inference that the final conclusion (which is based on the posterior distribution) is the result of combining two sources of information. One of these sources arises from the prior distribution, before the data were collected, and the other arises from the experimental data itself. The analysis performed here made use of very different prior distributions for the variance components. However, despite these different contributions from prior information, posterior inferences did not differ substantially. This is a reassuring conclusion, and it indicates that the experiment has enough informational content to override the influence of prior information to a large extent. In contrast with the other two methods of inference used in this study, the Bayesian approach to study response to selection takes into account the fact that other parameters (nongenetic effects and genetic variances) are being estimated from the same data. It also provides a Monte Carlo estimate of the marginal posterior distribution, which encapsulates all the information required for inferences about selection response. This posterior density is obtained without invoking analytic approximations or asymptotic results.

The reported estimates of heritability found in the literature for PS have been zero or very close to zero.

Thus, Haley and Lee (1992) reported an estimate of zero, and Bidanel *et al.* (1992) reported an estimate of 0.03 ± 0.03 for PS until the 30th day of gestation, using data from a French Large White pig line. The estimates obtained in the present study have a probability of $\sim$95% of being >0 in all cases.

It is clear that selection was effective for OR, as is to be expected from its high heritability. Selection for OR has also been effective in the only other experiment carried out in pigs (Johnson 1992), and in two experiments with mice (Bradford 1969; Land and Falconer 1969). Selection for PS has only been undertaken in mice (Bradford 1969, 1979), with positive results, but an experiment of selection for OR and PS in pigs does not seem to have improved PS (Casey *et al.* 1994). Our results show a low increment in PS, but the response, although low, is positive with a posterior probability of $\sim$95%. Further research will determine the correlated responses in litter size and other traits.

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